The Behavior of the Flowers of the Aguacatillo (Persea caerulea)

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In 1929, stimulated by the work of Stout (1927) on the flower behavior of the avocado in subtropical Florida and California, I made brief observations on the anthesis of avocado trees growing in tropical Panamá (Skutch, 1932). During subsequent years, while collecting plants in Central and South America, I have tried to find other species of the same family which exhibit a similarly complex mechanism for favoring cross-pollination. The Lauraceae is well represented in the forests of tropical America, and many species were collected; but most were tall trees that bore their flowers at such heights that it was not practicable to make continuous observations upon them.

So far as has been determined, no species of the great genus *Nectandra* exhibits the double anthesis of the avocado. On the other hand, it seems probable that the flowers of the wild avocado or yas (*Persea Schiedeana*) would behave more or less like those of its congener; but the only flowering trees of this species that I have seen were forest giants whose inflorescences were displayed far beyond reach. Aside from the avocado, the only member of the laurel family in whose flowers I have actually observed double anthesis is the aguacatillo (*Persea caerulea*).

The aguacatillo (Fig. 1) is a small or medium-sized tree with a full, shapely, rounded crown of glossy, ovate or elliptical leaves. The tallest specimens I have seen were about seventy feet high. It is a tree of the clearings, often growing in pastures, and in Costa Rica is abundant between two thousand and five thousand feet above sea-level, both on the Central Plateau and in the basin of El General. I have never found it in heavy forest. In El General it generally sheds its foliage at the height of the dry season in February. The dying leaves turn a fairly vivid red and make a bright display of autumnal colors, rare among tropical trees. Because they put forth their new foliage while shedding the old, however, there are usually far more green than red leaves upon the aguacatillo trees. They are, therefore, never quite so colorful as many northern trees in autumn. The name "aguacatillo," applied to this tree by the Costa Rican country people, is the diminutive of "aguacate" (avocado). The fruit measures about 9 mm. in diameter and contains a single seed, like a miniature avocado seed, surrounded by a very thin, green pericarp. No larger than a pea, the fruit is far smaller than any true avocado and is eaten by birds. The glossy, leaden-gray drupes ripen in June.

When they have shed, in their colorful manner, all or practically all of their old foliage and have put forth a fresh set of glossy leaves of a bright, vivid green, the aguacatillo trees begin to flower, usually in March in El

General. The dull yellowish flowers are borne in loose panicles which spring, on long peduncles, from the axils of the full-grown new leaves. Each blossom (Figs. 5 and 6), at full expansion, is about a centimeter in diameter. It consists of three very small roundish sepals, three alternating and much longer, narrowly ovate petals, an outer whorl of six stamens and an inner whorl of three, which are slightly longer and have narrower anthers, and alternate with the petals. Six small, roundish nectar-glands are in pairs at the bases of the three antesepalon stamens of the outer whorl. Three much larger, sagittate glands

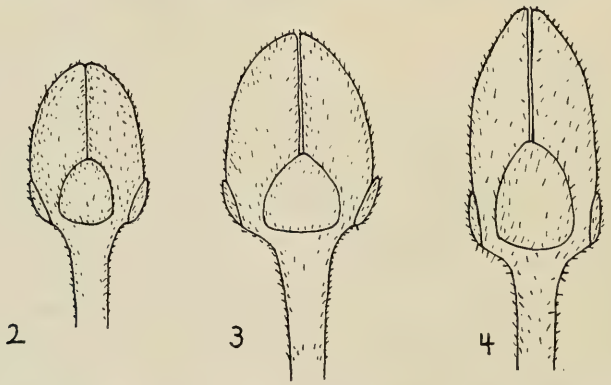
FIG. 1. Aguacatillo trees in March. Basin of El General, Costa Rica, altitude 850 meters.

alternate with the stamens of the inner whorl and hence lie above the petals. The flower has a single, simple pistil with a solitary ovule, unbranched style and oblique stigma. All parts of the flower are densely covered with a short, fine pubescence, except the glands, the anthers, and the pistil.

Each flower opens twice—on consecutive days. During the first opening (Fig. 5), the stamens lie against the petals, which are widely spread and lie all in one plane, and the anthers remain tightly closed. The pistil, however, stands up prominently in the center of the flower, with exposed and receptive stigma. Functionally the flower, during its first anthesis, is purely pistillate. After the termination of the first anthesis, the petals close tightly together again (Fig. 3); and during the period of closure the filaments of the stamens

elongate considerably, and there is a slight enlargement of all parts of the flower.

When it opens the second time (Fig. 7), the flower has an appearance quite distinct from that which it presented during its first anthesis. The petals bend outward even farther than before, until they become slightly reflexed. The stamens now no longer lie inconspicuously in contact with the petals, but stand up prominently in the center of the flower. The three innermost stand quite erect and parallel to each other; they rise above the stigma and almost conceal it. When the flower closed at the end of its first opening, they were shorter than the pistil; now they exceed it in length. The six outer stamens rise obliquely around the central group. Soon after the flower has opened, often before it has fully expanded, the anthers begin to open and to shed their pollen. Each anther dehisces by means of four elastic valves (Fig. 8), which

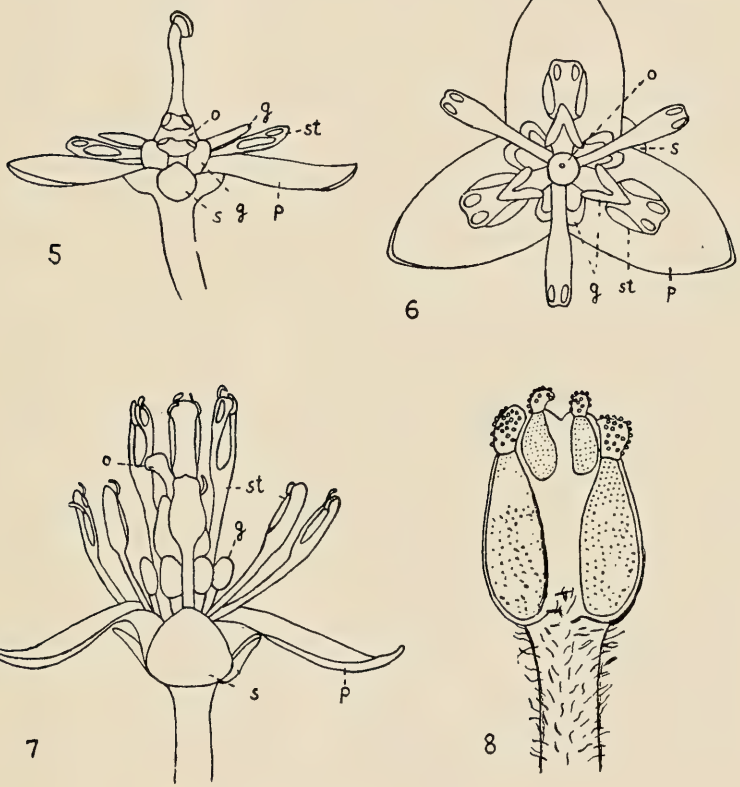


FIGS. 2-4.—FIG. 2. Bud of aguacatillo one day before opening. FIG. 3. Flower closed after first opening. FIG. 4. Flower closed after second opening. All x 5.

were already prominent on the closed anthers during the first expansion of the flower. There are two long valves for the outer anther cells, and between them two much shorter valves for the two inner anther cells. These valves become detached from the walls of the cells everywhere except at their narrow upper ends. They rise upward and outward until they stand above their respective cells and extend slightly above the end of the anther. They would project far more prominently if they did not shrink so strongly upon opening. The mass of pollen from each cell remains attached to the erstwhile inner surface of the valve, which finally becomes convex, and is thus prominently exposed at the tips of the stamens. The stigma, which was already discolored at the beginning of the second anthesis, soon becomes quite black and withered. It appears to be no longer receptive and is largely concealed by the stamens. During its second opening, the flower is purely staminate in function.

If one examines a number of trees at any time while their flowers are in full anthesis, he will find that the flowers of some appear to be in their first

opening while those of others are in their second opening. All the myriads of open flowers on any one tree are always found to be in the same stage—either all in the first opening or all in the second. Thus it is possible to recognize two classes of trees, which, following Stout's work (1927) on the avocado, we may designate "A" and "B." If these two kinds of trees are watched during



FIGS. 5-8.—FIG. 5. Flower of aguacatillo in first opening, from side. Note declined stamens and unopened anthers; x 5. FIG. 6. The same, from above; x 5. FIG. 7. Flower in second opening from side. Note ascending or erect stamens and opened anthers; x 5. FIG. 8. Dehiscent anther of the outer series of stamens, with lifted valves and escaping pollen; greatly enlarged. g = nectar gland, o = pistil, p = petal, s = sepal, st = stamen.

two consecutive days, with a few of their flowers marked with bits of thread so that they can be recognized in their different stages, a pattern of behavior can be formed.

Class A comprises those trees whose flowers open for the first time at dawn, and for the second time toward the end of the following morning. The petals of the hitherto unexpanded buds begin to separate from each other at

the end of the night, and before dawn (about 5:15 a.m. at this season) they are already slightly spread. The petals bend outward very slowly, and it may be two hours after they first begin to expand (or 7:15 a.m.) before they reach their fullest opening. The flowers are evidently functional, however, long before this. The fresh stigmas are sufficiently exposed to receive pollen when the flowers are half open, an hour after the sky begins to brighten. The nectaries begin to secrete their sweet fluid as soon as the sun falls upon the trees, and insects come to the flower.

Between 4½ and 5 hours after daybreak, or from about 9:45 to 10:15 a.m., according to the day and the individual tree, the flowers begin to close, with their anthers still tightly sealed and their pollen all unshed, but with their stigmas as a rule somewhat discolored. In from forty-five minutes to an hour after they display the first signs of closing, the flowers have all practically closed, although the final tight pressing together of the edges of the petals, until the once-opened flowers come to resemble larger buds (Fig. 3), takes place more slowly. Then there are always a few laggards—flowers which have been injured by the bites of insects, or are otherwise not in perfect condition—that fold up more slowly.

These once-opened flowers remain tightly closed until they begin to open on the following day at about the same time that they began to close after their first anthesis. They require about three-quarters of an hour to reach full expansion. On some trees, the anther-valves begin to lift and to expose the pollen before the petals have fully spread; but on others they open more tardily, and do not begin to rise until half an hour or more after the flower has completed its expansion. Simultaneously with the opening of these second-period flowers, another set of flowers on the same tree, which opened for the first time that same morning, are closing again. Soon after two o'clock in the afternoon, the flowers, which have shed all of their pollen, close for the second time, after an opening which lasted between three and four hours. By three o'clock or a few minutes later, if the afternoon is dry and warm, as it usually is at this season, all but a few laggards have closed (Fig. 4). On wet afternoons the closing of the flowers may be considerably delayed. Once folded up, they do not open again. Those which fail to be pollinated, or at least fail to be fertilized, fall in their entirety after lingering on the tree for a few days, during which they remain tightly closed. Those whose ovaries begin to develop into fruits—apparently always a small minority—shed only the perianth and the stamens.

If the flowers of all of the aguacatillo trees in any neighborhood behaved exactly as those whose history has been followed, it would be very difficult for them to be pollinated; for at the time their stigmas are receptive there would be no pollen shed, and while they are shedding their pollen, there would be no stigmas in condition to receive it. A necessary part of this complex mechanism is a second class of trees, Class B, whose floral behavior is com-

plementary to that of the first. The flower buds of the trees of Class B expand for the first time between ten and eleven o'clock in the morning, at the same time that the flowers of the trees of Class A are opening for the second time. Probably because of the higher temperatures which prevail at this hour of the day, they reach their full expansion more promptly than the Class A flowers at their first opening; and their stigmas are ready to receive the pollen which the Class A flowers, open for the second time, now begin to shed.

The transfer of pollen from flower to flower is effected by the small insects which come in large numbers to the abundant nectar secreted by the floral glands. In flying from a tree of Class A to one of Class B, they may carry the pollen grains to the latter. The flowers of Class B close at approximately the same time in the afternoon as those of the other class. Their period of closure is considerably shorter, for they open again at the following dawn, only fifteen hours after they folded together at the end of their first opening. The valves of their anthers begin promptly to rise, and before the sun has appeared they are already shedding their pollen. This the insects may now carry to the stigmas of the newly opened flowers of neighboring trees of Class A. Thus the two kinds of aguacatillo trees reciprocate: during the early morning the Class B trees supply pollen to those of Class A; and during the middle of the day, the Class A trees furnish pollen for the stigmas of the flowers of their neighbors of Class B.

The flowers of Class B make their second and final closing at the same time that a new set of flowers on the same trees is opening for the first expansion, and at the same time that the first-period flowers of the Class A trees are closing and the second-period flowers of these trees are opening. The interval between ten and eleven o'clock in the morning is the time of greatest activity of the flowers of the aguacatillo trees, for then all of them are either opening or closing, and each individual tree changes, for a period, from functionally pistillate to functionally staminate, or the reverse.

The opportunities for self- or close-pollination of the aguacatillo flowers are very limited. Because one of two different sets of flowers on the same tree opens while the other is closing, it is not impossible that the pollen from a second-period flower of a Class A tree, which opens its anther-valves promptly, may be carried to the stigma of a first-period flower of the same tree that is slow in closing. Similarly, on a tree of Class B, lingering pollen of a second-period flower may possibly be transferred to the stigma of a first-period flower which has just been exposed by the separation of its petals. But because of the close synchronization of the opening and closing of the different sets of flowers, and because of the brief period during which the transfer of pollen from anther to stigma of the flowers of the same tree is at all possible, it seems unlikely that many close-pollinations occur.

The foregoing account of the behavior of the aguacatillo flowers is based upon observations made at Rivas, in the basin of El General, on the Pacific

slope of southern Costa Rica, at an altitude of 2800 to 2900 feet above sea-level, in the middle of March, 1937. In order to learn something of the relative abundance of the two classes of trees, I took a census of all those in the immediate vicinity. Most had low branches within reach of the ground. But even when all the branches of the tree were high, the flowers could be classified as either in the first or second opening at any given time by examining through eight-power binoculars those which stood in profile against the sky. Of 29 trees which I classified, 16 belonged to Class A and 13 to Class B. It seems that the two kinds of trees occur in approximately equal numbers.

SUMMARY

Each flower of the aguacatillo opens twice—on consecutive days. During the first opening the stigma is receptive; the stamens lie inconspicuously against the petals with anthers tightly closed. During the second opening, the stamens stand up prominently and the anther-valves lift to expose the pollen; but the stigma appears to be no longer receptive. Thus in its first opening the flower is, in function, purely pistillate; in its second, staminate.

According to the behavior of their flowers, two classes of trees are recognized. Class A comprises trees whose flowers open for the first time at dawn, remain expanded with receptive stigmas for four or five hours, then close late in the morning. Twenty-four hours later they open again and shed their pollen. The periodicity of Class B flowers is complementary to that of Class A flowers. Their first opening, with receptive stigmas, occurs late in the morning, when Class A flowers are expanding the second time and shedding their pollen. These Class B flowers open the second time early the following morning and expose pollen which may be carried to Class A flowers in their first anthesis. Thus, early in the morning, Class B trees supply pollen for Class A trees, whereas, in the middle of the day, the Class A trees furnish pollen for those of Class B. Because all the flowers on the same tree open and close almost simultaneously, self- or close-pollination appears to be rare. Insects, attracted by the abundant nectar from the floral glands, are the principal agents of pollination.

Trees of the two classes are found in approximately equal numbers.

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